Reference: *Biol. Bull.* 172: 30–45. (February, 1987)

THE BODY PLAN OF THE CYPHONAUTES LARVA OF BRYOZOANS PREVENTS HIGH CLEARANCE RATES: COMPARISON WITH THE PLUTEUS AND A GROWTH MODEL

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Abstract

The cyphonautes larva of bryozoans is anomalous among ciliary suspension feeders with upstream particle capture. This is because the length of the ciliated band that produces the feeding current does not increase disproportionately relative to body length during larval development and growth. Comparisons with previous studies of other upstream collectors (mostly the pluteus of the echinoid *Dendraster excentricus* or other echinoplutei) demonstrated a striking deficiency in feeding capabilities of the cyphonautes. (1) In comparison to the pluteus the ciliated band generating the feeding current of the cyphonautes was short both absolutely and relative to larval body size as protein. (2) During larval growth, the length of the ciliated band of the cyphonautes decreased relative to protein in the whole body whereas the length of ciliated band of the pluteus was nearly isometric with body protein. (3) The ratio of metabolic capacity (by electron transport system assay) to protein content was similar for the advanced stage pluteus and cyphonautes. If respiratory rate is proportional to metabolic capacity in these larvae, then the cyphonautes does not compensate for low feeding capacity by reduced respiratory rate. (4) The velocity of the current across the ciliated band and the length of lateral cilia was similar for the cyphonautes and pluteus. Therefore, maximum clearance rates per unit length of ciliated band were not unusually high for the cyphonautes. (5) The cyphonautes was inferior in rate of capture of small (2 μm) spheres relative to 10 μm spheres in comparison to plutei feeding on the same suspension. (6) The pluteus and cyphonautes were similar in the maximum sizes of spheres ingested. (7) In two experiments the cyphonautes was more selective of spheres flavored by incubation with the alga *Dunaliella tertiolecta* than was the pluteus. (8) Different patterns of allometric growth of ciliated bands were incorporated in a growth model based on the difference between allometry of gain in organic carbon through feeding and loss of organic carbon through respiration. The model predicted that a cyphonautes form required a much greater concentration of food than a pluteus form to gain the same organic material in the same time. Thus the cyphonautes proved inferior to the pluteus in quantitative measures of capacity for suspension feeding. The highly conservative differences in larval body plans result in differing capabilities for feeding that are likely to influence larval growth rates and the evolution of life histories.

Introduction

The cyphonautes is the only known feeding larval form of bryozoans. The cyphonautes creates a feeding current with a band of lateral cilia much like the lateral cilia

Received 21 August 1986; accepted 25 November 1986.

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of adult bryozoans, other larval and adult lophophorates and the larvae of echinoderms and enteropneusts (Atkins, 1955; Strathmann, 1971, 1973, 1982; Strathmann *et al.*, 1972; Strathmann and Bonar, 1976; Winston, 1978; McEdward, 1984, 1986b). In other animals with this arrangement of cilia and upstream capture of particles, the ciliary band increases disproportionately as the animal grows, with loops of the band increasing in number or length. In contrast, the two bands of lateral cilia in the cyphonautes remain simple curved bands; length of the bands of lateral cilia increases in proportion to body length rather than surface area or tissue volume. The cyphonautes has unusual features that might affect quantitative measures of feeding capability. The bands of lateral cilia are within a mantle cavity (Atkins, 1955) and particles are captured by a sieve of laterofrontal cilia upstream from the lateral cilia (Strathmann and McEdward, 1986). Therefore we examined several features of the cyphonautes for comparison with the better known pluteus larvae of echinoids to answer the following questions. (1) Does the protein content or metabolic rate of the cyphonautes indicate an unusually low quantity of tissue for a larva of its size and thus account for the short band of lateral cilia? (2) Do velocities of particles crossing the bands of lateral cilia indicate faster feeding currents and hence higher clearance rates per unit length of ciliary band? (3) Are the cyphonautes larvae relatively more efficient than plutei at retaining small particles? (4) Could the cyphonautes larvae capture unusually large particles relative to their body size?

The answers to these questions supported predictions based on comparative morphology and indicated that the cyphonautes larval form is not well designed for high rates of ingestion from low concentrations of food. Implications for growth were derived from a model in which allometric changes in uptake of organic carbon were predicted from allometry of ciliated band length and in which allometric changes in losses of organic carbon were predicted from allometry of respiratory capacity. The results predict that cyphonautes larvae require much higher concentrations of food than do plutei to grow at the same rate. Slow larval growth as a consequence of larval body plan may have influenced the evolution of bryozoan life histories.

Materials and Methods

Eggs and earliest stage cyphonautes larvae were obtained at Friday Harbor, Washington, by letting colonies of *Membranipora membranacea* spawn into seawater with 0.0001 *M* EDTA (methods from C. Reed, pers. comm.). Cyphonautes larvae at more advanced stages were collected from the plankton. Larvae were maintained in the laboratory within a few degrees of ambient sea temperature, which ranged from 8°C in early spring to 13°C in late summer. The cyphonautes larvae from the plankton could not be identified to species with certainty but were most likely *Membranipora membranacea.* Those that metamorphosed to ancestrulae could be identified as *Membranipora,* and the most abundant *Membranipora* species near the San Juan Islands is presently thought to be *M. membranacea.*

The plutei of the sand dollar *Dendraster excentricus,* used in feeding experiments for comparison with cyphonautes larvae, were in most cases reared from eggs and sperm in the laboratory by methods described by Strathmann (1971). Those in the experiments with 5 and 10 μm spheres were obtained from the plankton. Other larval echinoderms, ophioplutei and bipinnariae, were obtained from the plankton.

Dimensions of the larval body were obtained by three-dimensional digitization as described by McEdward (1984, 1985). Body length and apical height were defined as shown in Figure 1. The measured ciliated band length was doubled to account for the two ciliated ridges. Surface area was taken as twice the projected area of the body outline in lateral view. Relative volume was obtained as the product of maximum thickness (from valve to valve in region X, Fig. 1) and projected area.

Exponents of the general allometric equation ($Y = aX^b$) were calculated by Bartlett's nonparametric method (Simpson *et al.*, 1960). The 95% confidence intervals were calculated empirically by nonparametric bootstrapping techniques (Efron, 1979; Diaconis and Efron, 1983). If the isometric exponent fell outside the confidence interval then the difference between the calculated exponent and the isometric exponent was statistically significant.

Protein content was measured by using the Coomassie brilliant blue G-250 dye binding assay method of Bradford (1976) and Sedmak and Grossberg (1977). Electron transport system (ETS) activity was measured using the methods of Owens and King (1975). The artificial electron acceptor in this reaction is 2-(p-iodophenyl)-3-(p-nitrophenyl)-5-phenyl tetrazolium chloride (INT). Aqueous extracts of larvae were prepared according to the methods of McEdward (1984).

Lengths of cilia were measured from cyphonautes larvae taken from a single sample during September 1985. Larvae were sorted live, relaxed with isosmotic $MgCl_2$, and then killed with formalin highly diluted with seawater. Because many cilia lay at an angle to the plane of focus, only the cilium that appeared to be longest was measured for each larva. Because many cilia approached the longest observed in each larva, picking the apparently longest cilium for each larva could only slightly overestimate the length of cilia. Poor orientation of many cilia would have resulted in an underestimate of cilia lengths if the mean of a random sample had been taken. Precision for cilium lengths is about ± 1 μm. Lengths of the locomotory (coronal) cilia were the same on anterior and posterior loops of the corona.

Films were taken with a high speed 16-mm cinecamera (Redlake Locam) at about 100 or 60 frames/s. A timing light placed a spot on the margin of the film every 0.01 s for more exact calculation of the time between frames. Larvae were held for observation in a *cul de sac* formed by pieces of broken coverglass between the cover glass and slide. Because the cilia generating the feeding current are within the mantle cavity and currents from the locomotory coronal band dominate the flow outside the mantle cavity, we were not concerned with drag from the walls of the glass cage. The velocity measurements were made on a temperature-controlled stage (Cloney *et al.*, 1970) with the slide cooled to about 12°C. The larvae had been maintained in the laboratory at about 10°C.

The particles used to test efficiency of capture of small particles were the polystyrene divinylbenzene spheres that are used in calibrating electronic particle counters. The spheres were suspended in seawater, dissociated by sonication in a water bath, and counted in a hemacytometer before final dilution to test concentrations. Larvae were introduced to a gently stirred suspension with known concentrations of particles of two sizes. After 12 minutes feeding was terminated by preservation in formalin buffered with $CaCO_3$. The gut contents were counted with differential interference contrast optics. The relative rates of particle capture are an estimate of relative efficiency of capture, but because transfer of larvae into the particle suspension disturbs feeding for an undetermined and probably variable time, the absolute rates of capture are not maximum feeding rates.

Polystyrene divinylbenzene spheres were also used to test capacity for qualitative selection of particles. For this test spheres of each size were incubated overnight with either seawater or with algal cells (*Dunaliella tertiolecta* or *Thalassiosira weissflogii*) that had been centrifuged and resuspended in seawater. Larvae were then introduced to suspensions in which one size of particle had been incubated with algae and the other with seawater only. For a more detailed description of this method, see Rassoulzadegan *et al.* (1984).

Spheres of another polymer (trade name Sephadex) were used to test for maximum sizes ingested. These spheres ranged from $\sim$20 to 60 μm in diameter. The

TABLE I

Larval dimensions for cyphonautes larvae of four sizes

	Stage 1	2	3	4
	n 5	16	5	10
Body length (μm)	155 (±10)	341 (±5)	526 (±15)	649 (±9)
Apical height (μm)	138 (±9)	267 (±4)	329 (±7)	394 (±5)
Height/length	0.90 (±0.03)	0.79 (±0.01)	0.62 (±0.01)	0.61 (±0.00)
Thickness (μm)	43 (±2)	68 (±5)	113 (±5)	143 (±4)
Band length (μm)	123 (±7)	361.00 (±13)	577 (±31)	644 (±24)
Surface area (10^4 μm^2)	3.6 (±0.4)	14.4 (±0.4)	28.8 (±1.2)	43.2 (±1.2)
Relative volume	8.0 (±1.1)	49.9 (±4.2)	163.9 (±13.9)	308.2 (±10.2)

Mean values (±SE).

spheres were soaked in seawater with *Dunaliella tertiolecta* for four hours; the algal suspension was decanted twice, and the spheres were soaked for another hour in seawater. The larvae were introduced to the suspension for 19 minutes and then preserved in buffered formalin. The diameters of spheres in the guts were measured with an ocular micrometer. To check for preservation artifacts, we compared fresh and formalin preserved subsamples of the stock suspension. Preservation and storage for more than a month had no effect on the size frequency distribution of the spheres.

For a model of growth based on estimated stage specific gains and losses of organic carbon, the coefficients and exponents of allometric equations were obtained by a model I regression (Sokal and Rohlf, 1981) through the logarithms of mean values for each stage. For isometric relationships the coefficient was the mean of ratios of values.

RESULTS

Ciliary band length relative to body size and shape

The cyphonautes larvae remained roughly triangular throughout growth, but the shape of the triangle changed. Apical height increased slower than body length (Table II). The steady decrease in the height:length ratio (Table I) resulted in longer but squatter larvae in later stages (Figs. 1, 2). Since thickness changed in proportion to body length, surface area increased more slowly with respect to volume than would be expected if later stages were geometrically similar to early larvae (Table II).

The cyphonautes has several bands and groups of cilia. The bands that generate the feeding current through the mantle cavity are the lateral cilia on a pair of ridges separating the upstream (inhalant) and downstream (exhalant) portions of the mantle cavity (Figs. 1, 2). Hereafter "band length" refers to the sum of the lengths of the two ridges because this is the total length of the bands of lateral cilia that generate the feeding current.

Band length of the cyphonautes was nearly isometric with body length. Mean band lengths and mean body lengths were 123 μm and 155 μm for the smallest measured size category and 644 μm and 649 μm for the largest (Table I). Ciliated band length increased in proportion to body length and in proportion to the linear component of volume (Table II).

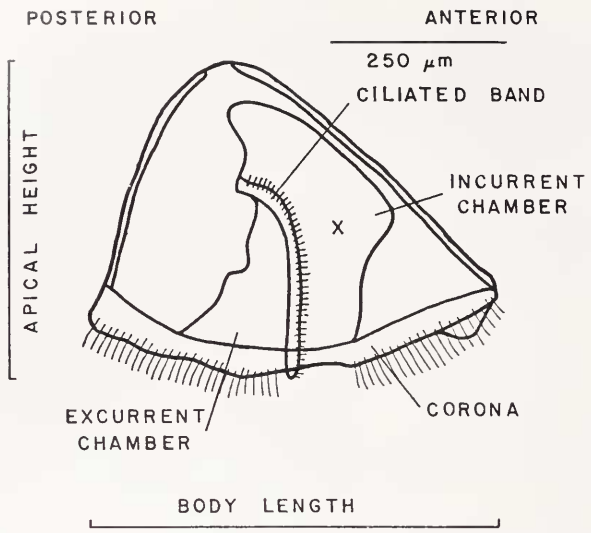

FIGURE 1. Positions of measurements on the cyphonautes.

To compare the cyphonautes with the pluteus we used the protein content of the larvae as a measure of larval size. Protein content of the larva increased in proportion to the cube of body length: 79 ng for a cyphonautes 341 μm long (n = 2) and 610 ng for a cyphonautes 649 μm long (n = 3). Protein content also increased in proportion to larval volume (Table II). Since band length did not increase relative to body length or volume, the band length decreased relative to protein content of the whole cyphonautes during larval growth (Table II). This was in contrast to the pluteus of *D. excentricus,* in which the ciliated band increased in proportion to larval volume, protein content, and ETS activity of the whole larva during development from the 4 to 8 armed stage (McEdward, 1984). In this pluteus, the protein content increased relative to ciliated band length only during the 8 armed stage, when the rudiments of post-metamorphic juvenile structures were developing.

If larval tissue increases relative to band length, then do metabolic needs increase relative to clearance rate? The ETS assay yielded 1.75 nmols INT h^{-1} $larva^{-1}$ for the

TABLE II

Exponents (b) of the general allometric equation ($Y = aX^b$)

Y	X	b	95% confidence interval	Isometric b
Apical height	Body length	0.64	0.57–0.71	1.00
Thickness	Body length	0.93	0.78–1.10	1.00
Band length	Body length	1.03	0.94–1.10	1.00
Protein	Body length	2.91	2.38–3.72	3.00
Protein	Volume	0.99	0.68–1.34	1.00
Surface area	Volume	0.58	0.53–0.64	0.67
Band length	Volume	0.37	0.32–0.41	0.33
Band length	$Volume^{0.33}$	1.11	0.99–1.25	1.00
Band length	Protein	0.39	0.21–0.60	1.00

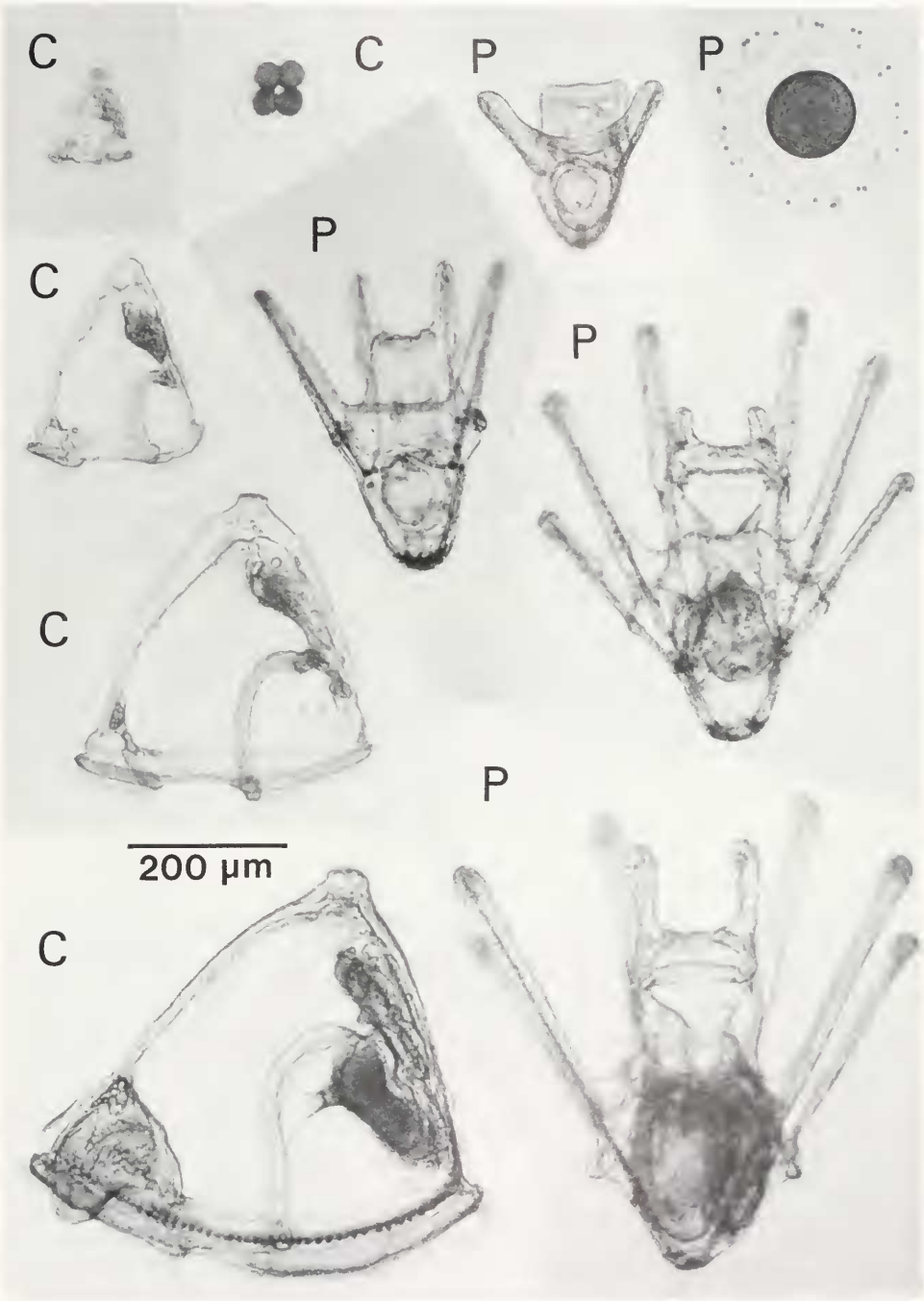

FIGURE 2. Change in size and form of a developing cyphonautes (C) of *Membranipora* and developing pluteus (P) of *Dendraster excentricus*. All embryos and larvae to the same scale.

TABLE III

Lengths of cilia and larvae in μm

Length of larva along open edge	Lateral cilia	Coronal cilia
320	21	38
330	20	40
470	21	48
540	19	57
600	21	57
	mean 20	

late stage cyphonautes, whose protein content was 610 ng larva^{-1} and body length was 649 μm. This ratio of metabolic capacity to protein was similar to the ratio for late stage plutei of *D. excentricus* (protein 600 ng larva^{-1}; ETS 1.44 nmols INT h^{-1} larva^{-1}; larval length 699 μm) (McEdward, 1984). Metabolic capacity is likely to be approximately proportional to metabolic rates. If it is, low metabolic rate does not compensate for the low clearance rate of the cyphonautes.

Increase in length of cilia and larvae

Coronal cilia increased in length as the larva increased in length, but length of lateral cilia remained constant (Table III). These cilia lengths suggest an increase in volume flow of water per unit length of the locomotory coronal band as the larvae increase in size but little if any increase in volume flow per unit length of the food capturing ciliated ridge as larval size increases. Cilia lengths of food collecting bands of *D. excentricus* are 20 to 25 μm long and do not increase during larval development (McEdward, 1984). The cilia producing the feeding currents are therefore similar in length and in constancy of length in both larval forms.

Particle velocities at the bands of lateral cilia

To compare velocities of feeding currents of the cyphonautes to previous measurements on the pluteus, we trapped cyphonautes larvae and filmed the passage of 5 μm spheres between the two bands of lateral cilia. Under the conditions of observation, the cyphonautes larvae retained and ate few particles and thus had a low clearance rate, but they maintained a fast current through the mantle cavity. We did not include any particle tracks in which more than two frames elapsed as the particle crossed the band because particles were sometimes arrested on the upstream side of the band and our object was to use velocities of particles as indicators of water velocity past the bands of lateral cilia. Some particles crossed the band in a single interval between frames (1/60 s) with a mean velocity of 1.7 mm/s (n = 16). If currents were only intermittently fast enough to carry particles across the band in one frame interval, this would be a biased estimate of velocity of the feeding current, but estimates with more frames may have included particles momentarily detained by latero-frontal cilia or other cilia. For particles crossing the band in two intervals between frames, the mean velocity upstream was 1.0 mm/s, and the mean velocity downstream was 1.4 mm/s (n = 38). The upstream velocity was significantly lower than the downstream velocity (Wilcoxon matched pairs signed ranks test, $P < 0.005$). Some particles crossed in two intervals, but the midpoint position was obscured; their mean velocity was 1.3 mm/s (n = 22). The grand mean was 1.3 mm/s (n = 76).

TABLE IV

Relative rates of ingestion of spheres of 10 μm and 2 μm diameter

	Number of larvae	Total 10 μm ingested	Total 2 μm ingested	Ratio clearance rates (10 μm/2 μm)
*Cyphonautes 490 to 480 μm length	6	76	8	57
**Dendraster excentricus* 4 armed pluteus	20	567	205	16.6
**Cyphonautes 270 to 490 μm length	9	45	5	90
***Bipinnaria*	1	100	35	29
***Cyphonautes 260 to 430 μm length	19	117	37	32
****Dendraster excentricus* 6 armed pluteus	20	757	280	27

* Larvae with 30/μl of 2 μm and 5/μl of 10 μm spheres for 12 min.

** Larvae with 20/μl of 2 μm and 2/μl of 10 μm spheres for 15 min.

*** Larvae with 30/μl of 2 μm and 3/μl of 10 μm spheres for 10 min and 2 μm spheres flavored with *Thalassiosira weissflogii*.

The proportions of 10 μm and 2 μm spheres ingested were significantly different from the proportions in suspension (G test, $P < 0.001$). Larvae with the same number of asterisks were in the same suspension.

Overall, the velocity of currents past the lateral cilia of the cyphonautes larva was similar to velocities of 1.3 and 1.7 mm/s past the ciliated band of plutei of *Lytechinus pictus* at room temperature (Strathmann *et al.*, 1972; Emlet, 1983). The feeding current of the cyphonautes was as fast or perhaps slightly faster than the current of plutei. Faster currents do not compensate for the short ciliated band of the cyphonautes.

Capture efficiency for small particles

Are cyphonautes larvae exceptionally efficient in retaining small particles? We compared the relative rates of ingestion of 10 μm and 2 μm spheres by cyphonautes larvae and by plutei of *Dendraster excentricus* and a bipinnaria (Table IV). The cyphonautes larvae were never much better and usually worse than the echinoderm larvae in the retention of the smaller spheres. Cyphonautes larvae retained the 2 μm spheres at much lower rates than 10 μm spheres even when the 2 μm spheres were flavored by previous incubation with a suspension of algal cells (Table IV). Capture of smaller food does not compensate for the lower clearance rates of the cyphonautes.

Limits on the maximum size of particles captured

Could cyphonautes larvae capture and ingest larger particles than those taken by other larvae with upstream capture? To determine the maximum size of particle that could be ingested, we fed echinoplutei, ophioplutei, and cyphonautes larvae a suspension of spheres for which the mean size was near the maximum size that the larvae could ingest (Table V). A sample of 50 spheres from the suspension (first row of Table V) is included for comparison with spheres ingested by the larvae (subsequent rows). Advanced stages of the cyphonautes and plutei with four to eight arms captured particles of about the same mean size. The mean size for the largest 10% of particles ingested was also similar for the advanced stage cyphonautes and for plutei. Sizes of particles ingested increased with larval size for each type of larva tested, but sizes were comparable for larvae of similar lengths. (The mean midline lengths of 4 armed *D.*

TABLE V

Maximum size of spheres ingested by larvae feeding in the same suspension for 19 minutes

	Number larvae	Spheres counted	Mean ± S.D. μm	Range μm	Mean of largest 10% ingested
Suspension sample	—	50	45.1 ± 11.8	22.1–70.7	—
Cyphonautes 330–400 μm length	6	8	28.2 ± 2.6	24.3–33.5	33.2
Cyphonautes 460–580 μm length	10	30	31.1 ± 5.6	18.8–46.4	42.0
Dendraster excentricus 4 armed pluteus	10	36	30.1 ± 4.4	22.1–38.7	38.2
Dendraster excentricus 8 armed pluteus	10	62	31.6 ± 4.8	21.0–43.1	40.6
Ophiopluteus 6 armed	3	10	28.2 ± 4.1	21.0–34.3	34.3
Ophiopluteus 8 armed	7	39	30.4 ± 6.9	12.1–44.2	42.3

excentricus and 6 armed ophioplutei were 280 μm and 300 μm. The mean midline lengths of the 8 armed plutei were 330 μm.) Capture of larger food does not compensate for the low clearance rates of the cyphonautes.

Does the width of the mantle cavity ultimately limit the size of particles that can be captured by the cyphonautes? No particles this large were ingested in this experiment. Near the center of the upstream side of the mantle cavity (point X in Fig. 1) the depth of the mantle cavity is 143 μm in a cyphonautes larva of 649 μm body length (Table I), but the ingested particles were less than 50 μm. Either the maximum width of the incurrent path is much narrower elsewhere, or the width of incurrent openings greatly overestimates maximum sizes ingested.

Selection of particles on the basis of quality rather than size

Is the cyphonautes more discriminating than other larvae with upstream retention of particles? Larvae were fed a suspension of 5 and 10 μm diameter spheres in equal concentration but with spheres of one size flavored by incubation with cells of *Dunaliella tertiolecta.* All the larvae tested ingested 10 μm spheres at higher rates than 5 μm spheres, but the preferential ingestion of 10 μm spheres was greater when they were flavored than when the 5 μm spheres were flavored (Table VI). In these experiments the effect of flavoring on relative ingestion rates was greater for the cyphonautes than for the echinoderm larvae. Further experiments would be needed to confirm the generality of this result because only one algal species was tested and the effect on ingestion rates by the echinoderm larvae was not pronounced. In contrast, in similar experiments by Rassoulzadegan *et al.* (1984) on larvae of *D. excentricus* the effect of a flavoring from a culture of algal cells was greater and was sufficient to reverse preference for 5 and 10 μm spheres. Differences in discrimination may exist, but establishing both the existence of differences in selectivity and the consequences of such differences for larvae under natural conditions will require a more extensive set of comparisons.

A model relating allometric change in form to growth rates

An important consequence of larval feeding is growth, because faster growth results in a shorter planktonic period and presumably therefore less loss of larvae

TABLE VI

Selection of particles on the basis of presence or absence of flavor acquired by incubation with Dunaliella tertiolecta

	Number of larvae	Flavored bead	Total 10 μm ingested	Total 5 μm ingested	Ratio of ingestion rates (10 μm/ 5 μm)
*Cyphonautes	18	5 μm	55	36	1.5
**Cyphonautes 290 to 590 um length	24	10 μm	141	51	2.8
**D. excentricus*	1	5 μm	78	38	2.1
***D. excentricus* 8 armed pluteus	1	10 μm	90	31	2.9
*Bipinnaria	2	5 μm	31	13	2.4
**Bipinnaria	4	10 μm	130	37	3.5
***Cyphonautes	25	5 μm	198	175	1.1
****Cyphonautes 500 to 630 um length	26	10 μm	245	58	4.2
****D. excentricus*	7	5 μm	704	419	1.7
*****D. excentricus* 8 armed pluteus	7	10 μm	654	288	2.3

* and **: Larvae with 5/μl of 5 μm and 5/μl of 10 μm spheres for 12.5 min.
*** and ****: Larvae with 5/μl of 5 μm and 5/μl of 10 μm spheres for 10 min.
Larvae with the same number of asterisks were in the same suspension.

through transport or predation. Can observations on ciliated band length (here proportional to maximum clearance rate) and metabolic capacity (assumed proportional to losses from respiration) be converted to predictions about larval growth at different concentrations of food? We expect allometric changes in feeding capacity to be a major determinant of duration of the planktonic period from first feeding to competence for settling or metamorphosis but the relationship is not simple. Here we explore some of the simplest possible models for the relation between allometry of band length and duration of the larval period.

We wish to explore implications of allometric changes in form for duration of the larval period. Our reasoning is similar to that of Pütter (1920) and von Bertalanffy (1957) except that we are more willing to sacrifice accurate description of growth by fitted curves (Ricker, 1979) for the sake of analysis of effects of form. For this reason we have used the general form of their model of growth in organic material (w) with time (t) as

$$dw/dt = Bw^b - Aw^a \qquad (1)$$

but without their restrictive assumptions about the value of the exponents b and a. This permits comparisons based on observed allometric relationships of different larval forms.

If clearance rates are approximately proportional to lengths of ciliated bands and if respiratory rates are approximately proportional to capacity of the electron transport system then rate of growth can be modelled as the difference between two allometric equations as in equation (1) where Bw^b is rate of intake of materials and Aw^a is rate of loss of materials. Integrating this expression from the starting organic content to the organic content when the larva is competent to metamorphose gives the minimum planktonic period (T).

$$T = \int_{w_0}^{w_1} dw/(Bw^b - Aw^a) \qquad (2)$$

This can be solved by several substitutions. First let $u = (A/B)w^{a-b}$ and rearrange to get

$$T = C \int_{u_0}^{u_1} (u^c du)/[u(1 - u)]$$

where $C = [(B/A)^{(1-b)/(a-b)}]/[B(a - b)]$ and $c = (1 - b)/(a - b)$ and then let $v = u/u_1$ and $v' = u/u_0$ and rearrange to get

$$T/C = u_1^{(c-1)} \int_0^1 [u_1 v^{(c-1)} dv]/(1 - u_1 v) - u_0^{(c-1)} \int_0^1 [u_0 v'^{(c-1)} dv']/(1 - u_0 v') \quad (3)$$

The solution to equation (3) is in Gradshteyn and Ryzhik (1980, p. 286, #3.197.3) in terms of a Beta function and Gauss' hypergeometric function

$$T/C = B(c, 1)[u_1^c F(1, c; c + 1; u_1) - u_0^c F(1, c; c + 1; u_0)]$$

when $c > 0$. This expression simplifies to

$$T = C[(A/B)(w_1)^{a-b}]^c \sum_{n=0}^{\infty} [(A/B)w_1^{a-b}]^n/(c + n)$$

$$- C[(A/B)(w_0)^{a-b}]^c \sum_{n=0}^{\infty} [(A/B)w_0^{a-b}]^n/(c + n) \quad (4)$$

The condition that $(1 - b)/(a - b) > 0$ limits the range of values for the allometric exponents for this method of relating larval form to planktonic period.

A special case of interest is $c = 1$ because this occurs when $a = 1$, and the allometric exponent for losses through respiration and excretion is likely to be close to 1 for many ciliated larvae. When $c = 1$, equation (4) simplifies further (Gradshteyn and Ryzhik, 1980, p. 44, 1.513.4) to become

$$T = [1/(A(1 - b))] \ln [(B - Aw_0^{1-b})/(B - Aw_1^{1-b})] \quad (5)$$

When the exponents a and b both equal 1, the result is simply

$$T = [1/(B - A)] \ln (w_1/w_0) \quad (6)$$

Equations (4), (5), and (6) apply under restricted conditions. There must be growth throughout the range of sizes. Suspended food must be ingested and assimilated at rates proportional to the length of the ciliated band that produces the feeding current. Material must be lost from the body at a rate dependent on size but independent of concentration of food. A realistic and quantitative prediction would only be possible for the range of concentrations of food that results in nearly constant respiration and clearance rates. Both respiration and clearance rates vary with food concentration for a variety of suspension feeders. Several types of echinoderm larvae reduce their clearance rates above about 1000 cells/ml of *Dunaliella* spp. (Strathmann, 1971; Lucas, 1982). Concentrations of food could also affect respiration (Fenaux *et al.*, 1980) and assimilation by these larvae. The situation is complicated for *Dendraster excentricus* by the development of longer arms (and therefore a longer ciliated band) at lower concentrations of food (I. Boidron-Metairon, pers. comm.). The following calculations are therefore for gross comparisons between the cyphonautes and pluteus forms.

Application of the model to the cyphonautes of *Membranipora* and pluteus of *Dendraster excentricus* requires additional assumptions about measurements and conversion factors. Table VII gives mean values for body protein, the electron transport system assay, and length of ciliated band. Table VIII gives coefficients and expo-

TABLE VII

Measures of size and metabolic capacity for the cyphonautes of Membranipora *and pluteus of* Dendraster excentricus

Larva	Cyphonautes			Pluteus			
Stage	New	Small	Advanced	4 arm	6 arm	8 arm	8 arm with rudiment
Protein (μg)	0.013*	0.078	0.61	0.079	0.123	0.169	0.599
ETS (nmol INT/h)	—	—	1.75	0.093	0.21	0.22	1.44
Ciliated band (mm)	0.12	0.36	0.64	1.45	2.50	4.20	6.90

* Protein value from egg.

nents for the allometry of rates of gain and loss in relation to body organic content in terms of organic carbon. To get from Table VII to Table VIII we made the following assumptions and calculations.

Organic carbon in the body was assumed to be 0.75 times the protein, a conversion taken from an assumed ratio of 17.8% nitrogen in the protein in the whole body and from a ratio of carbon to nitrogen of 4.2 for zooplankton (mean among phyla) (Omori and Ikeda, 1984). This conversion would underestimate organic carbon in later stages if later stage larvae store more fat. The measured protein content per egg was assumed to be equal to the protein in the early stage cyphonautes. Protein probably declines so that organic content of the early cyphonautes was overestimated. As a result growth of the cyphonautes was underestimated, and this biases the comparison in favor of the cyphonautes.

We ignored excretory losses and assumed that the respiratory rate was directly proportional to the ETS assay, which was assumed to be proportional to the protein measurement. For comparison of cyphonautes and pluteus we used the mean of (ETS)/(protein) for the five available points for both types of larvae (Table VII). We assumed 2 nmol INT = 1 nmol O_2 (Immers and Runnstrom, 1960; DeVincentiis *et al.*, 1966), a value within the range observed for other zooplankton though toward the lower end of the range (Omori and Ikeda, 1984), and for conversion to organic carbon assumed a respiratory quotient of 1. For the pluteus we also used the regression through the mean values for the four stages. The coefficients and exponents assumed for isometric and allometric rates of loss are in Table VIII.

To convert ciliated band length to a rate of clearance and assimilation, we assumed that the volume flow per mm of band was a 20 μm length of cilium times half a tip velocity of 1.7 mm/s times 1 mm and that the assimilation efficiency was 60%, a value within the calculated range for larvae of *Mytilus edulis* (Sprung, 1984) and above some estimates for gastropod veligers (Pechenik, 1980). The coefficient B in equation (1) was partitioned into the product of B_1 and the concentration of food (F). For comparison of cyphonautes and pluteus we assumed allometric relationships between ciliated band length and body organic content. For the pluteus we also tried an isometric relationship between band length and body organic content because this relationship is approximately isometric for much of larval development (McEdward, 1984). Coefficients (B_1) and exponents (b) for assumed allometric and isometric relations are in Table VIII.

With these values and equations (4), (5), and (6), we calculated the concentration of food required for growth through the feeding larval stages in three weeks. The cyphonautes required about ten times the concentration of food required by the pluteus (Table VIII). This result was not changed when rates of loss by the pluteus were

TABLE VIII

Results of a growth model predicting concentration of food required for growth from organic content W_1 to W_2 in μg C in 21 days

Larva	B_1	b	A	a	W_1	W_2	F
			Observed growth				
Cyphonautes	0.868	0.424	0.364	1	0.00945	0.458	0.27
Pluteus	12.3	0.730	0.364	1	0.0592	0.449	0.025
Pluteus	12.3	0.730	0.584	1.321	0.0592	0.449	0.026
Pluteus	22.1	1	0.364	1	0.0592	0.449	0.021
			Same growth				
Cyphonautes	0.868	0.424	0.364	1	0.045	0.45	0.27
Pluteus	12.3	0.730	0.364	1	0.045	0.45	0.026

The growth equation is $dW/dt = B_1FW^b - AW^a$ with F the concentration of food in μg C/ml, B_1 and b estimated from ciliated band length, and A and a estimated from metabolic capacity. See text for the estimates of allometric shifts in loss and gain and other assumptions.

assumed to be allometric or when rates of gain by the pluteus were assumed to be isometric, though such changes did produce changes in shapes of growth curves, as expected (see Fletcher, 1975). The result was also not changed when the same interval of growth was assumed for both cyphonautes and pluteus. When concentrations of food are limiting, the cyphonautes should be at a substantial disadvantage relative to the pluteus in rate of growth.

Development times in the model were extremely sensitive to concentration of food, however. This sensitivity is highly unrealistic. Rates of development and growth of plutei of *Dendraster excentricus* do not decrease in proportion to decreased concentrations of phytoplankton (Paulay *et al.*, 1985), and rates of growth and development of larvae of the seastar *Acanthaster planci* are similar in the food poor waters of the Great Barrier Reef and much higher rations in culture (Olson, 1985). These and many other observations indicate that adjustments in rates of loss or gain of organic material with different concentrations of food are important for these larval forms. Because our model lacks compensatory adjustments to different food supplies, the model may exaggerate the predicted differences in food required for similar growth rates.

Ciliated band length and metabolic capacity can be combined for another comparison of the cyphonautes and pluteus forms. Volume of water cleared per volume of oxygen consumed is a measure of feeding efficiency from which one can extrapolate to a concentration of food at which ingestion would equal respiratory losses, a break even point if clearance and respiration rates were constant and assimilation efficiency 100% (Jørgensen, 1966). With conversion factors similar to those for the growth model except for 100% assimilation efficiency, the late stage cyphonautes "broke even" at 130 μg C/l, the late stage pluteus with a rudiment at 10 μg C/l, and the earlier 4 to 8 armed stage plutei at about 3 to 4 μg C/l. Because this calculation assumed that respiration does not decline at low ingestion rates, the predicted concentrations of food required to avert starvation are probably too high. This simpler comparison also predicts a relative disadvantage for the cyphonautes form at low concentrations of food.

Simple models predict large differences in growth of the cyphonautes and pluteus because of differences in the lengths of ciliated bands that produce the feeding currents.

Discussion

The cyphonautes larva of bryozoans has an anomalously short band of lateral cilia that generate the feeding current. The current velocity at the bands of lateral cilia, the length of lateral cilia, and the relative rates of capture of large and small food particles are similar to those for plutei, which have a much longer ciliated band at a similar body size. The contrast extends to other suspension feeders with upstream capture. The lateral cilia of the cyphonautes are no longer than those of adult bryozoans, phoronids, and brachiopods or those of larval phoronids, brachiopods, enteropneusts, and echinoderms. The cyphonautes does have one feature as yet unobserved in related suspension feeders with upstream capture. It filters particles with a sieve of laterofrontal cilia (Strathmann and McEdward, 1986). However, it appears that no expansion of capabilities is associated with this sieving mechanism. Because the cyphonautes has no apparent means of compensating for its low rate of clearing water of suspended particles, it appears to be at a disadvantage relative to other forms in regard to feeding in waters with low concentrations of food.

Because the cyphonautes larval form occurs in both ctenostome and cheilostome bryozoans, it is probably the ancestral larval form for the class Gymnolaemata (Nielsen, 1971), yet most species in this class now lack a feeding cyphonautes stage. One hypothesis for the scarcity of feeding larvae in the group is that the ancestral larval form had a poor capability for feeding and growth under conditions common in coastal waters. Against this hypothesis is the observation that cyphonautes larvae nevertheless have broad geographic and seasonal occurrence and are common in waters low in phytoplankton. Moreover, the eggs of bryozoans with cyphonautes larvae can be quite small. In the San Juan Islands *Membranipora membranacea* has an egg diameter of about 60 μm, smaller than that of the local echinoderms (Emlet *et al.*, 1986) and phoronids (Zimmer, 1964; Emig, 1974). Organic content increases with increasing egg size among species with feeding larvae from several phyla (Strathmann and Vedder, 1977), and the protein per egg for *Membranipora membranacea* (0.013 μg) is less than that for four species of local echinoids (.024–.148 μg) (McEdward, 1986a). Parental investment per offspring is probably lower for *Membranipora membranacea* with its cyphonautes larva than for co-occuring echinoids and phoronids that use similar larval ciliated bands in larval feeding but have larval forms with apparently greater capacity for clearing particles from suspension. With small eggs and low clearance rate, the larval bryozoan is predicted to have an unusually long planktonic period with associated risks. Yoshioka's (1982) best fit for a planktonic period from field data off Southern California was about four weeks, not extraordinarily long for a larva. We cannot yet resolve these apparent discrepencies.

The combination of poor design for foraging, small initial larval size, and broad geographic occurrence suggests that the cyphonautes larval form has some other redeeming qualities. Any capabilities in feeding that may have been missed in this study would have to be substantial to compensate for the short ciliated band. Another hypothesis is that the cost of slow growth may be low. The only field estimate of mortality rates of the cyphonautes (Yoshioka, 1982) was no lower than those for bivalve veligers and other small larvae (reviewed in Strathmann, 1985), though all of these mortality estimates depended on assumptions about sampling and were subject to large errors. Slow larval growth might be advantageous if there was no advantage to

more growth before settlement and if there was an advantage to a long precompetent period, but it is difficult to imagine situations in which these two conditions are commonly met (Strathmann, 1985). Thus possible compensatory benefits from the cyphonautes form are not yet apparent.

A protective shell is not a constraint on length of ciliary band in all larval forms. A shell is combined with an extensible feeding organ in larvae of inarticulate brachiopods, which have separate lateral cilia and upstream capture of food as does cyphonautes, and in larvae of gastropod and bivalve molluscs, which differ in that they capture food downstream using a band of compound cilia. Though the cyphonautes form and short ciliated band are conservative, functional or developmental constraints on this form have not been demonstrated.

In conclusion, the cyphonautes larval form has an anomalously poor capacity for suspension feeding. This is predicted to result in slower growth than in other larvae with upstream capture by cilia when food is scarce. A compensating advantage is not yet apparent.

ACKNOWLEDGMENTS

NSF grants OCE8008310 and OCE8400818, the Kilham Foundation of the University of Alberta, and the Friday Harbor Laboratories of the University of Washington supported this study. We are grateful to T. Daniel for integrating growth equations and for other help and advice from B. Hargreaves, C. D. Harvell, R. Highsmith, C. G. Reed, M. F. Strathmann, and R. L. Zimmer.

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